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Estimation of Light-use Efficiency of Terrestrial Ecosystems from Space: A Status Report

NICHOLAS C. COOPS, THOMAS HILKER, FORREST G. HALL, CAROLINE J. NICHOL, AND GUILLAUME G. DROLET

A critical variable in the estimation of gross primary production of terrestrial ecosystems is light-use efficiency (LUE), a value that represents the actual efficiency of a plant's use of absorbed radiation energy to produce biomass. Light-use efficiency is driven by the most limiting of a number of environmental stress factors that reduce plants' photosynthetic capacity; these include short-term stressors, such as photoinhibition, as well as longer-term stressors, such as soil water and temperature. Modeling LUE from remote sensing is governed largely by the biochemical composition of plant foliage, with the past decade seeing important theoretical and modeling advances for understanding the role of these stresses on LUE. In this article we provide a summary of the tower-, aircraft-, and satellite-based research undertaken to date, and discuss the broader scalability of these methods, concluding with recommendations for ongoing research possibilities.

Keywords: light-use efficiency, gross primary production, remote sensing, biochemical, satellite

Understanding the amount of atmospheric carbon dioxide (CO_2) absorbed and released by terrestrial ecosystems is critical for climate change research. Terrestrial ecosystems absorb approximately 60 gigatons (Gt) of carbon annually, whereas autotrophic and heterotrophic organisms release approximately the same amount of carbon back into the atmosphere. The estimated annual turnover of approximately 120 Gt is a magnitude larger than anthropogenic carbon emissions, and as a result, there is a need for a better understanding of the dynamics of carbon fluxes between the biosphere and atmosphere if we are to quantify potential changes as a result of greater atmospheric CO_2 concentrations (Luo and Reynolds 1999).

Terrestrial carbon absorption is known as gross primary production (GPP), or the gross carbon uptake of vegetation through photosynthesis. Gross primary production can be defined as the product of the absorbed photosynthetically active radiation (APAR), which is the absorbed solar radiation between 400 and 700 nanometers (nm) wavelength, and light-use efficiency (LUE), which represents the actual efficiency of a plant's use of absorbed radiation energy to produce biomass (Monteith 1977). Light-use efficiency is determined by the most limiting of a number of environmental stress factors that reduce a plant's photosynthetic capacity at a given time (Demmig-Adams 1990). The nature of this limitation of photosynthetic capacity can be short term, such as when it is caused by stresses imposed by

photoinhibition; other factors, such as soil water deficits and suboptimal temperatures, can cause longer-term reductions that can lower photosynthetic capacity even after the actual stress event has ended.

Spatially continuous modeling of terrestrial carbon cycling requires model parameterization of the land surface (Hall and Sellers 1995), which can be performed regularly only through remote sensing. Global estimates of the incoming photosynthetically active radiation (PAR) are typically derived from top-of-the-atmosphere measurements of solar radiance using satellite observations combined with optical modeling approaches (Sellers et al. 1995). The fraction of PAR that is absorbed by plants to provide the energy input for the photosynthetic reaction process (fPAR) depends almost entirely on the absorption surface; that is, the leaf area of the plants. Empirical studies (Tucker 1979), large field experiments (Sellers and Hall 1992), and theoretical work (Sellers et al. 1996) have demonstrated that APAR is closely related to the difference between top-of-the-canopy reflectance in the visible and near-infrared (NIR) regions of the electromagnetic spectrum, and is often approximated using the normalized difference vegetation index (NDVI; Tucker 1979), an index composed of spectrally broad reflectance bands centered at red and NIR wavelengths.

Modeling LUE from remotely sensed data is carried out with the awareness that plant physiological properties are related to the biochemical composition of plant

foliage, which can be inferred from the often-narrow spectral properties of leaves and canopies (Hilker et al. 2007, 2008a). In the decades after the launch of the first Earth-orbiting satellites in the 1970s, the remote sensing community was limited by the number and width of the spectral wavebands available for spaceborne sensors, and observation frequencies of existing sensors were incapable of detecting the spatial and temporal variability of vegetation LUE. Research in past decades has led to the advent of high-spectral-resolution optical sensors that can be mounted on towers, aircraft, and satellites, and that are capable of detecting changes in leaf spectral properties with a high temporal frequency. These sensors have allowed the scientific community to revisit a number of existing approaches for modeling GPP and reassess the potential for using remotely sensed inputs, with the ultimate aim of developing GPP models driven solely by satellite-based observations (Running et al. 2004).

In this article we review these recent developments, in terms of the theoretical relationships between the underlying physiological and biochemical reactions and LUE, as well as in the modeling framework for understanding the role of short- and long-term stresses on LUE. We provide a summary of the tower-, aircraft-, and satellite-based research to date and discuss the broader scalability of these physiological and spectral relationships. We conclude with a series of recommendations for the ongoing validation exercises needed for the implementation of this methodology into an operational satellite-based product.

Leaf-level physiological stress behavior

Plants absorb radiation energy principally through chlorophyll but also through carotenoid pigments contained in green plant tissue. In photosynthesis, a photon excites an electron of an absorbing pigment into an elevated state, thereby providing energy to the photosynthetic system. This energy can then be directed along three competing pathways within the chloroplast. A first, almost immediate response to light absorption is chlorophyll fluorescence, which is the reemittance of photons into space. Since part of the radiation energy is lost in the absorption process, fluorescent light is produced at longer wavelengths than that of the absorbed light. Despite being a largely physical response under little biological control, chlorophyll fluorescence depends on the amount of energy consumed by the two remaining pathways, photochemical and nonphotochemical quenching. Photochemical quenching refers to the transfer of energy to the reaction center of photosystem II (PSII), where it is used to split water into oxygen (O_2) and H^+ and ultimately reduces $NADP^+$ (nicotinamide adenine dinucleotide phosphate) into NADPH, thereby providing energy for the photosynthetic dark reaction (figure 1; Demmig-Adams 1990). Alternatively, nonphotochemical quenching occurs when there is a lack of available resources to support photochemical quenching and the subsequent dark reaction, which results in an accumulation of H^+ ions and subsequent

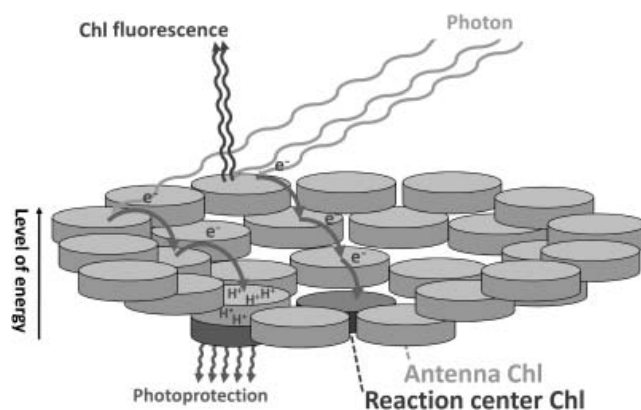


Figure 1. Diagram of fluorescence and photoprotection processes in the light-harvesting complex of photosystem II. Chl, chlorophyll. Source: Adapted from Hilker and colleagues (2008b).

acidification of the thylakoid membrane. This acidification triggers the de-epoxidation of a group of leaf pigments, known as xanthophylls, located in the pigment-protein complexes of photosynthetic membranes (Björkman and Demmig 1987). During this reaction, the xanthophyll pigment violaxanthin is converted rapidly into zeaxanthin through the intermediate antheraxanthin. The structures of antheraxanthin and zeaxanthin accept excessive energy and safely dissipate it as heat in order to prevent damage to the photosynthetic apparatus (Demmig-Adams 1990). This process, which is also referred to as photoprotection, is a major component of nonphotochemical quenching, or thermal energy dissipation. Recently, a second photoprotective mechanism, the lutein (or Lx) cycle, was discovered (Bungard et al. 1999) and is believed to work in parallel to the xanthophyll cycle, at least within some shade species.

Photosynthetic LUE is the proportion of the energy used in the photochemical reaction process (photochemical quenching) to the amount of energy directed through the two nonphotochemical pathways. Under optimal conditions, plants are able to use most absorbed energy for photosynthesis, but under high light conditions, the photochemical reaction process is usually limited by a shortage of one or more resources, including site-related factors such as nutrient availability, water supply, and temperature. Because the three energy pathways (photosynthesis, fluorescence, and photoprotection) compete, any increase in the activity of one of these processes will result in a decrease in the yield of the other two. Consequently, measurement of fluorescence and nonphotochemical quenching can be used to determine LUE in leaves.

Canopy-level physiological stress behavior

Canopy-level LUE, in contrast to leaf-level LUE, can be defined as the sum of the photosynthetic efficiency of the individual leaves on a tree. This integrated photosynthetic efficiency is the result of microscale changes in the radiation regime to which an individual leaf is exposed, as well

as the physiological adaptations made in response to the more general characteristics of light conditions experienced over time. For example, the illumination condition affecting a forest canopy at a given time and location is constantly changing and depends on numerous factors, such as the incoming PAR (measured in watts per square meter), cloudiness (quantifiable as the ratio of direct to diffuse sky radiation; Hilker et al. 2008a), and between- and within-crown shading effects (determined by the canopy structure and sun position). The physical, physiological, and biochemical responses of a leaf to its immediate radiation environment depend on its level of adaptation to those conditions. Adaptations occur in a number of different ways. First, there are differences in nutrient and water supply between individual leaves as the plant optimizes its available resources to maximize overall productivity and growth (Sellers et al. 1996). For instance, the nutrient flow in the upper canopy is generally higher than in leaves located in the lower tree crown because leaves in the upper canopy are generally exposed to much higher radiation levels and therefore exhibit a higher photosynthetic potential. Second, morphological differences in leaf thickness and the number of stomata ensure the greatest possible use of photosynthetic potential. These differences allow sun-exposed leaves to tolerate higher levels of radiation without reducing their photosynthetic efficiency, and enable shaded leaves to photosynthesize even under low-light conditions. As a result, the exposure of shade-tolerant leaves to direct illumination, such as during sunflecks, will reduce their photosynthetic capacity much more significantly than it would the capacity of sun-adapted leaves. Finally, photosynthetic capacity at the crown level is also subject to physical constraints—in particular, the force of gravity—that make the supply of nutrients, especially water, increasingly difficult with greater height.

As a result, stress levels within an individual tree crown often follow a vertical gradient, causing elements in the upper crown to be exposed to, on average, higher stress levels than those located lower in the canopy. Consequently, a detailed understanding of the interactions between canopy structure and canopy stresses is a basic requirement for vertical and horizontal scaling of remotely sensed estimates of LUE (Hilker et al. 2008a).

Direct measurement of LUE

A variety of approaches exist to estimate changes in the pigment concentration of vegetation in response to excessive light.

Measuring quantum yield and fluorescence. Detection of chlorophyll fluorescence has typically included passive methods (Carter et al. 1990) and laser-induced active methods (Ananyev et al. 2005). Active fluorescence measurements track changes in the chlorophyll fluorescence yield using laser pulses. These pulse-modulated measuring systems contrast the yield of chlorophyll fluorescence

under steady-state (dark) illumination conditions with fluorescence under a short, saturating flash delivered up to 10 meters (m) away from the target. A number of available commercial instruments can perform these types of measurements to successfully measure photosynthesis (Rascher et al. 2000). However, the short distance between the laser and the vegetated surface restricts the analysis to individual leaves in accessible canopies (Ananyev et al. 2005), with a few notable exceptions (e.g., Cecchi et al. 1994). Researchers have achieved detection of a solar-induced fluorescence (SiF) signal (Buschmann and Lichtenthaler 1999), and others have modeled the effect using radiative transfer approaches (Zarco-Tejada et al. 2000). As this measurement approach is based on passive detection of the chlorophyll fluorescence signal, it may provide a basis for larger-scale assessment of LUE (Corp et al. 2006). Under natural conditions, however, this technique is more challenging, as the fluorescence emitted by vegetation represents less than 3% of the reflected light in the near-infrared part of the electromagnetic spectrum. Consequently, the spectral sensitivity of any detection device must be very high for these regions of the electromagnetic spectrum, where solar radiation is greatly reduced as a result of atmospheric absorption (i.e., the so-called Fraunhofer lines; Meroni and Colombo 2006).

Indirect measurement of LUE using the eddy covariance method

One of the most commonly applied methods for indirectly measuring photosynthetic LUE is the eddy covariance (EC) technique, which determines carbon fluxes by the covariance between fluctuations in vertical wind velocity and the CO₂ mixing ratio in the air column above the canopy (Baldocchi 2003). The EC data provide integrated measurements of stand-level net ecosystem exchange (NEE) and, as a result, LUE can be determined indirectly using the Monteith approach:

$$\varepsilon = \frac{GPP}{APAR} \quad (1)$$

where ε is the photosynthetic LUE. Eddy covariance measurements are widely accepted for determining stand-level carbon fluxes and have been applied in numerous studies for investigating the dynamics of stand-level ecophysiological properties and for validating LUE models at leaf (Fleisher et al. 2006), stand (Nichol et al. 2000, 2002), and landscape scales (Running et al. 2004). However, a number of uncertainties and limitations remain when using the EC method. First, the area sampled by EC measurements (also known as the flux footprint) is usually restricted to a few hundred square meters, upwind from the flux tower, and its size and location vary over time depending on several factors, including wind speed and direction, height of the flux measurements above the canopy, and stand height and density. As a result, EC data cannot be used to measure LUE at a single tree canopy or small forest stand level. Second, the EC theory assumes steady environmental conditions and surface homogeneity within the observed area for at least the

footprint radius in the upwind direction (Baldocchi 2003), an assumption often violated by actual field conditions. Finally, and most importantly, GPP can be derived from net ecosystem production (NEP) only if ecosystem respiration is known:

$$GPP = NEP + R_d \quad (2)$$

where $NEP = -NEE$, and R_d is daytime ecosystem respiration (Jassal et al. 2007). Since measurements of R_d are possible only in the absence of photosynthesis, this value is derived from nighttime measurements of ecosystem respiration during those periods when wind speed is sufficiently high to allow adequate mixing of air in the column above the canopy (Jassal et al. 2007). Generally, the approach used to estimate R_d is to develop a model of the relationship between air or soil temperature and nighttime ecosystem respiration, and then apply this model to diurnal measurements of the temperature. Although this method is general practice for EC measurements, numerous studies have demonstrated the uncertainties related to extrapolating nighttime measurements of ecosystem respiration to daytime observations (Morgenstern et al. 2004).

Remote measurement of LUE

An avenue of research gaining increasing attention is the passive remote detection of chlorophyll SiF to remotely estimate plant physiological status, and notably, stress.

Measurement of solar-induced fluorescence from air- and spaceborne systems. Although most LUE research to date has been designed to detect decreases in net carbon assimilation rather than in LUE, the results reported in this section also show

promise for the direct estimation of LUE. SiF is the fluorescence emitted under constant illumination, without saturating flashes. A growing number of studies show that the emission of SiF is strongly correlated with CO_2 assimilation and stomatal conductance under variable irradiance conditions and during periods of stress (e.g., Flexas et al. 2002). Theoretically, the intensity of the SiF signal should be inversely correlated with the energy used for photosynthesis, and could therefore serve as a remote indicator of photosynthetic LUE (Baker 2008). Care must be taken, however, when interpreting the SiF signal, because the inverse correlation can be weakened as a result of faster energy dissipation in the xanthophyll cycle (Govindjee 1995). On the other hand, the measurement of parameters directly related to photosynthetic capacity is critical and will improve our ability

to explain short- and long-term photosynthetic responses to actual and predicted changes in environmental conditions.

The absolute SiF signal can be quantified from both leaf and canopy radiance data because chlorophyll fluorescence, under solar illumination, adds a weak signal to the reflected solar radiation (figure 2; Meroni et al. 2009). This SiF signal can be detected passively in the narrow dark lines of the solar and atmospheric spectrum where the irradiance is strongly reduced (the Fraunhofer lines). There are three main Fraunhofer features that can be used to estimate SiF: the H α feature as a result of hydrogen absorption in the solar atmosphere at 656.4 nm, and two telluric oxygen (O_2)–absorption bands in Earth's atmosphere, O_2 -B at 687.0 nm and O_2 -A at 760.4 nm. The required resolutions for SiF detection in these regions are 0.005, 0.1, and 1.0 nm full width at half maximum (FWHM), respectively. The rationale for the quantification of SiF is to exploit these absorption bands by determining the degree to which the bands “infill” by the fluorescing target relative to the reflectance continuum. Promising results have appeared in the last few years from such radiance-based approaches, through infilling of the atmospheric oxygen absorption band in the radiance spectra of field-based experiments (Corp et al. 2006). A number of these studies have analyzed data collected from custom-built instruments, including the passive multiwavelength fluorescence detector (PMFD; Ounis et al. 2001), which uses interference filters to measure the radiation coming from plant canopies as well as from calibrated white reference panels at the two O_2 absorption bands. Flexas and colleagues (2002) used the PMFD to track naturally induced variations in SiF and successfully related that information to the photosynthetic status of boreal forest canopies. In contrast to

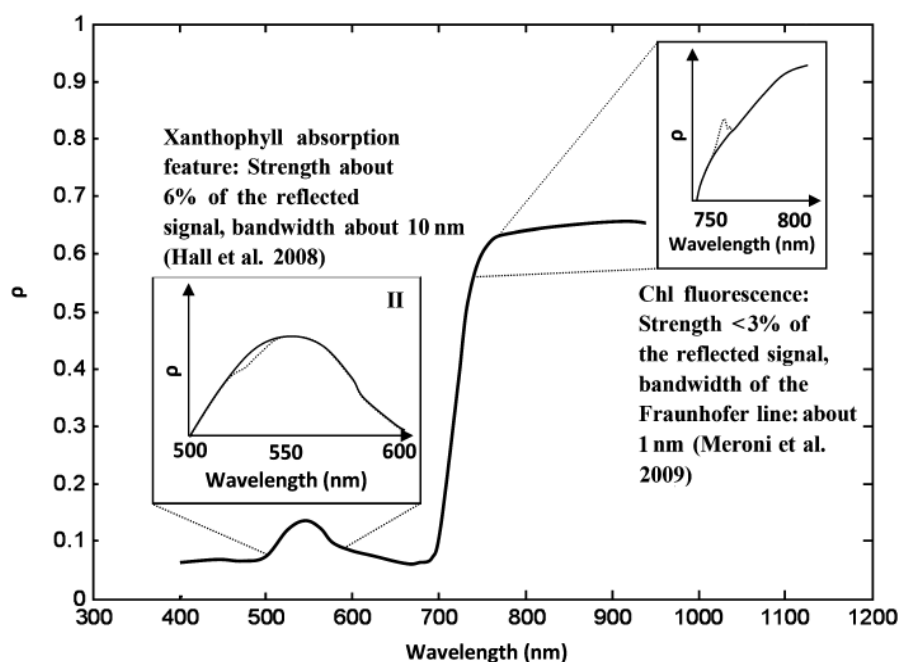


Figure 2. Changes in spectra at both photochemical reflectance index and fluorescence wavelengths of a stressed and unstressed leaf. Chl, chlorophyll; nm, nanometers.

the use of custom-built instrumentation for quantification of SiF, a number of studies have also tried using commercially available spectrometers, including the FieldSpec Pro (Analytical Spectral Devices Inc.), on a range of different species under varying stress conditions. A comprehensive review can be found in Meroni and colleagues (2009).

To date, the extension of this work to larger spatial scales has been limited by the inability of current systems to cover large areas. The shift in spatial scale as technologies move from ground to aircraft, and ultimately to satellite-based systems, adds further complexity to the quantification of the SiF signal, in part because of the influence of the atmosphere on this subtle physiological signal. A sophisticated approach for decoupling atmospheric influence from the SiF signal has yet to be developed, and to date, only site-specific relationships have been applied. Zarco-Tejada and colleagues (2003) demonstrated the utility of detecting SiF in the two O₂ absorption bands from hyperspectral CASI (compact airborne spectrographic imager, ITRES, Canada) data with a 7.5 nm FWHM. Using the infilling approach and a robust atmospheric correction scheme, they outlined the differing stress conditions of a corn crop under nitrogen treatment. Despite the spectral resolution being too coarse for sensitive estimation of SiF, the authors reported a good correlation between CASI-derived SiF and ground-based measurements of fluorescence.

In further work, Zarco-Tejada and colleagues (2009) used data from an airborne multispectral camera with narrow-band (1-nm FWHM) filters centered at the 757.5 nm and 760.5 nm bands, and four 10-nm-FWHM bands in the 400–800 nm spectral region, to examine the variability in SiF emission of orchard trees as a function of stress. The authors mapped SiF at a high spatial resolution (15 centimeters) and were able not only to discriminate well-watered trees from water-stressed trees but also found that SiF was highly correlated with ground-based fluorescence measurements and leaf-level net CO₂ assimilation rates. Successful retrievals of SiF and plant physiological status from airborne data have also been presented by Corp and colleagues (2006) for crop systems. In these studies, airborne data were acquired by the Aisa imaging spectrometer (Specim, Finland), and, following the application of the infilling method, researchers were able to discern the effects of different nitrogen treatments on corn crops.

Approaches based on reflectance rather than radiance data, through the computation of spectral indexes, can also be used to track changes in SiF, although they cannot quantify SiF emission in absolute physical units. These indexes work by exploiting the effect of SiF on the measured passive signal in the red edge region of the spectrum (650–800 nm), and a suite of indexes have been developed, with varying degrees of success. Typically, these indexes include one spectral band that is affected by SiF and another that is not. Solar-induced fluorescence is then estimated by normalizing the contributions of both the affected and unaffected bands. The SiF signal is further enhanced by calculating indexes from derivative indexes because the derivative

of the reflectance improves the detection of the subtle signal associated with SiF while minimizing confounding unrelated signals (Zarco-Tejada et al. 2003). Zarco-Tejada and colleagues (2000) showed in early work that reflectance and derivative indexes of SiF calculated from airborne CASI data were sensitive to the changing LUE at the canopy scale.

Sioris and Evans (2002) and others investigated the potential for detecting SiF from space using model simulations and demonstrated that the SiF signal should be detectable from an orbiting spectrometer. However, the only such satellite application to date was performed by Guanter and colleagues (2007), who successfully estimated SiF from vegetation using spaceborne images acquired by the medium-resolution imaging spectrometer (MERIS), aboard the environmental satellite (ENVISAT). Guanter and colleagues (2007) successfully retrieved SiF over a southern European site using atmospherically corrected data in the O₂-absorption features at 753.8 nm and 760.6 nm; the results compared well to retrievals made from an airborne imager (CASI), as well as ground-based measurements. The strong correlations between ground, aircraft, and satellite retrievals demonstrated that spaceborne estimation of SiF will be a feasible avenue for future exploration.

Measurement of the state of the xanthophyll cycle. A separate line of inquiry has focused on detecting the photoprotective mechanism from changes in leaf spectral reflectance resulting from the epoxidation of the xanthophyll cycle pigments. Spectrally, these changes manifest themselves in two narrow-waveband absorption features at 505 nm and 531 nm, which are directly related to the differences in the absorption spectra of violaxanthin, antheraxanthin, and zeaxanthin. Gamon and colleagues (1992) quantified the narrow absorption feature at 531 nm by comparing the reflectance at 531 nm (ρ_{531}) with that of a xanthophyll-insensitive reference band at 570 nm (ρ_{570}), yielding the photochemical reflectance index (PRI):

$$PRI = \frac{\rho_{531} - \rho_{570}}{\rho_{531} + \rho_{570}} \quad (3)$$

In this pioneering research, Gamon and colleagues (1992) demonstrated the principal connection between the epoxidation state of the xanthophyll cycle pigments and reflectance at both the leaf and plant levels (figure 2; Hall et al. 2008). The original index design was developed at the leaf scale for sunflowers, and since then numerous studies have demonstrated a logarithmic relationship between LUE and PRI. This relationship has since been confirmed over a wide range of species and conditions (Gamon 1997). Another study confirmed the usefulness of PRI as a predictor of LUE for more than 20 species, except for at extremely low light levels (Gamon 1997). More recent studies have confirmed these results (Guo and Trotter 2004). Barton and North (2001) found significant relationships between PRI and PSII efficiency for a range of different species; however, the relationship was affected by the xanthophyll pigment

concentration, which in turn is species dependent. Guo and Trotter (2004) suggested the application of a light-response curve to this relationship to account for those differences.

However, upscaling the initial successes of PRI from the leaf scale to individual canopies, and ultimately to regional and global scales, remains challenging. First, the temporal dynamics inherent in plant photosynthesis require frequent observations of vegetation status. From a satellite orbit point of view, this means observing a specific vegetated target under multiple illuminations and viewing conditions. These multiangular and multitemporal observations are then subject to bidirectional reflectance and scattering effects superimposed on the desired reflectance signal (Hilker et al. 2008a). For instance, the reflectance change in the PRI detection band is only about 7% (absolute reflectance units) of the total reflectance and thus difficult to recover in the presence of other factors that can cause variations in spectral reflectance of similar or larger magnitudes (Hall et al. 2008). Second, airborne or spaceborne sensors can provide only snapshots in time, determined by a given aircraft or satellite overpass (Sims et al. 2005). However, the temporal and spatial requirements for these observations to be considered representative of the physiological status of plant canopies are not well understood (Hall and Sellers 1995). Third, the relationship between PRI and LUE is species dependent; it also changes with age, canopy structure, pigment pool size, and leaf-area index (Barton and North 2001), making a spatial extrapolation of empirical findings difficult.

Upscaling of leaf-level PRI observations

Observations of PRI can be applied at a range of scales.

Near-surface approaches. Given the multiple dependencies of PRI, recent research has focused on near-surface remote sensing, typically using ground-based spectroradiometers suspended above a vegetated surface (e.g., a grassland, meadow, shrub, or forest). In these experimental setups, spectral radiance is acquired under a range of conditions more natural than those observed in laboratory-based experiments. This approach allows detailed studies of the factors affecting reflectance signal under natural conditions and at the stand level, thereby helping to explain and model the uncertainties associated with larger-scale observations from airborne or spaceborne imagery. As part of the Boreal Ecosystem-Atmosphere Study, Gamon and colleagues (1997) used an overhead tram system suspended between two towers to detect changes in trembling aspen (*Populus tremuloides* Michx.) spectral characteristics over a summer observation period. Another ground-based tram system has since been implemented in chaparral vegetation in southern California (Sims et al. 2005).

Leuning and colleagues (2006) designed and implemented a tower-based spectroradiometer scanning system that allowed spectra from the top of the forest canopy to be acquired and analyzed, and Hill and colleagues (2006) computed PRI from the spectra and compared it

with eddy-flux observations for the same period. Similarly, Hilker and colleagues (2007) developed a more advanced tower-mounted multiangular radiometer system (AMSPEC) to automatically measure canopy reflectance year-round and at different azimuth angles around the tower. These multiangular measurements help describe the anisotropy of the vegetation surface (Chen and Leblanc 1997), and as a result, PRI can be characterized as a function of the sun-observer geometry (modeled using bidirectional reflectance distribution functions [BRDF]), the sky condition at the time of measurement, and the physiological status of the observed vegetation canopy (i.e., ϵ). Hilker and colleagues (2008a) found a strong, nonlinear relationship between ϵ and stand-level PRI in a Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *menziesii*) forest, thereby allowing for the first time a continuous, year-round tracking of LUE from spectral observations. Importantly, this work found a strong dependency of ϵ and PRI on canopy structure and shading effects, which further emphasized the need for multiangular measurements to determine PRI at a stand level (Hall et al. 2008, Hilker et al. 2008a). A further development of this technique (Hilker et al. 2009) added a number of different vertical zenith angles to allow for a more complete observation of the canopy BRDF and simulate the illumination conditions of overpassing satellites using near-surface observations.

Airborne observations. A number of studies using airborne sensors have been conducted to observe PRI at the stand and landscape levels. One of the difficulties associated with airborne observations is that they provide only a single snapshot in time (Sims et al. 2005) of a limited area, whereas the spatial and temporal variability inherent in LUE suggests the need for more continuous observations. As a result, airborne studies have largely been designed as an intermediate step to further investigate and validate the relationship between PRI and LUE, and observe the effects of the various dependencies of PRI when trying to scale up from the stand level to the small-region level.

Méthy (2000) demonstrated that airborne radiometric assessments of PRI are correlated with the photochemical efficiency (PSII), but introduce additional complexities such as a dependency on sun and observation angles, as well as background reflectance. Nichol and colleagues (2000, 2002) investigated the LUE of the Canadian boreal shield and a Siberian boreal forest during spring using a helicopter-mounted portable spectroradiometer system. Spectra were compared with half-hourly measurements of sensible heat, water vapor, and CO₂ exchange obtained from nearby EC measurements. Although good relationships between airborne and EC measurements were found for the Canadian site, only moderately strong relationships ($r^2 = 0.5$) were found for the Siberian study site, most likely because of rapid changes in the canopy understory during the observation period. In an attempt to bridge the spatial gap between near-surface and airborne remote sensing platforms, Chen

and Vierling (2006) used a tethered-balloon-mounted platform to evaluate canopy PRI over a grassland-conifer forest ecotone. Further interscale studies include the comparison of data acquired from the airborne visible infrared imaging spectrometer and near-surface observations obtained from a tram system (Rahman et al. 2001). The results showed a strong link between carbon fluxes and optical properties for investigated vegetation types.

Spaceborne observations. Very few studies have tried to estimate LUE from spaceborne sensors (Drolet et al. 2008, Goerner et al. 2009, Hilker et al. 2009); research has largely focused on data acquired from the moderate resolution imaging spectroradiometer (MODIS). The rationale for using MODIS hinges on the availability of a narrow detection band centered at 531 nm (band 11) and its daily revisit cycle, which allows frequent observations of changes in PRI. Although the MODIS sensors aboard both the Terra and Aqua satellites are probably the best available option at the moment, MODIS was not originally designed for this purpose. First, MODIS lacks a reference band at 570 nm, and second, band 11 (531 nm) operates at a fairly coarse spatial resolution of 1 km². Drolet and colleagues (2008) substituted the missing reference band by quantifying the changes in reflectance of MODIS band 11 using either MODIS bands 10 (483–493 nm), 12 (546–556 nm), or 13 (662–672 nm) (PR₁₀, PRI₁₂, PRI₁₃, respectively) as reference bands. Additionally, MODIS band 1 (620–670 nm) has been suggested as a substitute reference and has been tested over a Mediterranean oak stand (Goerner et al. 2009). Although these studies found relationships between MODIS observations and EC-measured ϵ , a number of key issues were identified (Drolet et al. 2008) using the MODIS sensor. First, a significant relationship between PRI and ϵ was found only for backscatter observations, suggesting that directional reflectance and shading effects overlapped and confounded the observed PRI signal. Second, MODIS-based PRI observations were strongly affected by atmospheric scattering effects, thus limiting the ability to observe the minor changes induced by physiological canopy conditions. Finally, the differences in the areas of observation (i.e., the pixel footprint) between the MODIS and EC-flux data within different satellite overpasses caused significant uncertainties and noise in the PRI-to- ϵ relationship. To overcome these issues, Hilker and colleagues (2009) proposed a new approach for determining LUE from MODIS by comparing the satellite observed reflectance with the tower-observed AMSPEC reflectance rather than with eddy covariance observations directly. This approach minimizes the directional reflectance effects by adjusting the sun-observer geometry of the two sensors using a BRDF model to transform the AMSPEC data. Additionally, atmospheric scattering effects were corrected using a novel multiangle implementation of atmospheric correction (Lyapustin and Wang 2005, 2009). This technique, together with a careful analysis of MODIS's varying footprint geometry, considerably improved the relationship

between spaceborne and tower measurements. A highly significant relationship between tower-measured and spaceborne PRI was found for forward and backscatter MODIS observations ($r^2 = 0.74$) using year-round observations. This technique is therefore a potential avenue for measuring LUE directly from spaceborne observations of PRI.

Future research directions

Research has shown that both fluorescence and photoprotection generate detectible leaf- and canopy-scale reflectance changes that are highly correlated with LUE at both the leaf and forest stand levels. Current research includes study of how these biophysical changes, with significant leaf- and forest-level reflectance correlations, can be used to quantify the degree of photosynthetic down-regulation in a spatially continuous mode. Future research directions could take the following forms.

Development of a theoretical (physically based) canopy-level model to predict reflectance changes at 531 nm. One of the basic research needs identified in this article is for the development of an improved understanding of the relationship between remotely sensed photochemical reflectance spectra and canopy-level down-regulation of LUE as it varies with sensor view and solar illumination conditions, forest stand geometry, and unstressed leaf optical properties. The ultimate goal of this research is to develop physically based models that are more generally applicable than the empirical studies used to demonstrate the general relationship between LUE and spectral observations.

There is as yet no physically based algorithm to robustly relate forest-level reflectance changes at 531 nm to down-regulation. Such algorithms need to be based on canopy reflectance models that account for the leaf-level reflectance changes as a function of photosynthetic down-regulation and that can scale these variations from the leaf up to the canopy level. Down-regulation in turn depends on incident PAR levels, which themselves vary throughout the canopy, being lowest in shaded portions and highest in directly sunlit areas. For a given level of incident PAR, down-regulation also depends on the availability of other resources required for photosynthesis, as well as species type (Barton and North 2001). In this regard, there are two limitations of existing canopy reflectance models: (1) None permits leaf-level optical properties to depend on leaf-level illumination conditions, and (2) leaf-level reflectance models that can compute reflectance changes as a function of down-regulation have not yet been developed. Until these limitations are addressed, algorithms will remain empirical, with model-forms and their coefficients based on EC tower-derived measures of vegetation LUE.

An intensive modeling effort will also lead to the development of a more comprehensive understanding of changes in resource allocation across the vertical profile of a forest canopy. Modeling will also help assess the impact of differing illumination conditions that can result in significant

physiological differences throughout the crown. The results of these efforts can then be compared with the significant work already undertaken on the extent of diurnal, seasonal, and annual variations on the vertical distribution of the leaf physiological attributes. The recent development of easily deployed, robust, automatic, remote spectral sensors (e.g., Garrity et al. 2010) to detect differences in leaf-level reflectance changes throughout a tree crown will provide additional important measurement technology, allowing linkages with existing studies on photosynthetic light saturation curves, chlorophyll fluorescence, and other similar measurements of canopy photosynthesis.

Validation tool for conventional EC approaches. As discussed throughout this article, a critical calibration and validation tool to assess the accuracy of predicted canopy LUE has been the comparison with EC-derived estimates, which have their own intrinsic uncertainties and limitations. One future direction could therefore be the more integrated use of PRI and other reflectance-based approaches with EC techniques to overcome some of the inherent limitations of both approaches. For example, reflectance data might be used to help quantify the spatial variation observed within the EC footprint—a method of removing bias in the CO₂ estimates. Secondly, as satellite-based LUE algorithms are developed, they will play a key role in the calibration and validation of models that use EC-based data sets.

Satellite-based applications. In addition to the development of improved theoretically based algorithms, we need satellite-based LUE algorithms to account for the fraction of shadow viewed by the satellite and also for the canopy illumination conditions at the time of observation. Sunlit leaves, which undergo the largest changes in reflectance at 531 nm, dominate the satellite-observed changes in canopy reflectance. However, the bulk canopy LUE is an average of the canopy, including both sunlit and shaded leaves. A sensor at a single view angle rarely measures the same sunlit-to-shaded ratio as that of the illuminated canopy. Thus, at a minimum, satellite approaches must account for the difference between what the sensor sees at a particular view angle and what the canopy sees at a particular illumination angle, and direct-to-diffuse ratio of incident radiance. So far, estimations of the fraction of shadow and sunlit leaves viewed by the sensor are achieved using mixture decomposition algorithms (Hall and Sellers 1995), provided shaded and sunlit end-member values are available by species. The actual fraction of shaded and sunlit leaves seen by the entire canopy is dependent on canopy morphology, illumination geometry, and the ratio of direct to diffuse radiation.

These illumination issues could be partly resolved through the use of multiangle remote sensing to measure the variation in the photochemical index (PRI) as a function of sensor view angle. Hall and colleagues (2008) showed that when reflectance of the sunlit and shaded leaves in a forest is equal, PRI is not dependent on the shadow fraction (or by

inference, the sunlit fraction) viewed by the canopy. Thus, when the canopy is not strongly down-regulated, a multi-angle measurement of PRI when viewing different shadow and sunlit fractions will not vary strongly with view angle; conversely, the variation in PRI with viewed shadow fraction will be related to the degree of down-regulation. However, this approach requires measurement of the canopy PRI at a number of sensor view angles during a sufficiently brief time interval, when LUE is relatively constant. Such sensors exist, however, and have been flown on both aircraft and spacecraft (e.g., Barnsley et al. 2004).

Satellite-observed reflectance depends upon—in addition to canopy reflectance—the aerosol optical thickness of the atmosphere. Aerosols affect satellite measurements of canopy reflectance through their effects on atmospheric path radiance and aerosol optical depth at the time of the satellite acquisition. These atmospheric effects must be removed or minimized in order to stabilize the satellite PRI signal for spatial and temporal variations in the atmosphere. One challenge with most atmospheric correction algorithms is that they require a priori information, as only one orbit observation is used to solve for aerosol optical thickness (AOT) and surface reflectance. A common solution to this issue is the retrieval of AOT over dark objects (Levy et al. 2007); however, this does not allow for multiangular observations. More recently, a new aerosol-surface reflectance retrieval algorithm was developed (Lyapustin and Wang 2009) that calculates AOT from the differences in path length observed by multiorbit acquisitions. This method has been demonstrated to stabilize the MODIS PRI signal over a growing season for a wide range of atmospheric conditions and view angles (Hilker et al. 2009) and may therefore be a possible way to remove atmospheric effects from PRI observations.

Following MODIS, the acquisition of the critical wavelengths from satellite-based radiometers is less clear. MODIS's operational replacement, the visible infrared imager/radiometer suite, currently is not configured with a 531-nm spectral band (<http://jointmission.gsfc.nasa.gov/science/VIIIRSScience.html>). Other future missions, however, such as HypsIRI, one of NASA's decadal survey priorities set for launch late next decade, offer more promise for space-based estimation of LUE. HypsIRI is an imaging spectrometer that measures at wavelengths ranging from the visible to the shortwave infrared, with a spatial resolution of 60 m at nadir, and a three-week revisit time. HypsIRI has 10-nm spectral bands suitable for the calculation of PRI. Similarly EnMAP, to be launched by the German Aerospace Center in 2013, is also an imaging spectrometer that allows calculation of PRI at 30-m spatial resolution on a four-day repeat cycle and offering significant potential.

With increasing confidence in our ability to estimate LUE at a variety of scales and under a variety of illumination and view angle conditions, we can also consider the development of a more comprehensive integration of spatial and temporal predictions of LUE within existing or even new process-based forest production models. A range of models

known as “light-use efficiency models,” such as 3-PG (Physiological Principles Predicting Growth; Landsberg and Waring 1997), FOREST-BGC (Running and Coughlan 1988), BIOME-BGC (Heinsch 2006), and BIOMASS (McMurtrie et al. 1990), all use an implementation of the Monteith modeling approach, driven primarily by vegetation light absorption, which in turn determines potential photosynthesis rates. In these approaches, a maximum LUE value is set, either on a species or biome basis, and is then reduced by modifiers that represent the degree to which photosynthesis is inhibited by environmental factors. The modeled modified LUE represents the realized LUE of the forest canopy in response to its environment. Clearly, linkages that incorporate a variable LUE derived from remote sensing into these existing forest production models are a logical and critical next step.

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Nicholas C. Coops (nicholas.coops@ubc.ca) and Thomas Hilker are with the Department of Forest Resource Management at the University of British Columbia, in Vancouver. Forrest G. Hall is with the Joint Center for Earth Systems Technology at the University of Maryland Goddard Space Flight Center, in Greenbelt, Maryland. Caroline J. Nichol and Guillaume G. Drolet are with the School of GeoSciences, University of Edinburgh, in the United Kingdom.